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Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands

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Running headline: macro/micro-scale determinants of species abundance in drylands

ABSTRACT

1. Disentangling the interplay between species-specific environmental preferences and micro- and macro-scale determinants of species abundance within plant communities remains challenging. Most existing studies addressing this issue either lack empirical data regarding species interactions and local abundances or cover a narrow range of environmental conditions.
2. We merged species distribution models and local spatial patterns to investigate the relative importance of key macro- (aridity) and micro- (facilitation and competition) scale determinants of plant species abundance along aridity gradients in drylands worldwide. We used information derived from the environmental niches of species to evaluate how species-specific aridity preferences modulate the importance of such factors to drive species relative abundance.
3. Facilitation and aridity preferences were more important than competition to explain species local abundances in global drylands. The specialization of communities (i.e. their compositional shifts from species with a large range of aridity preferences towards only aridity specialists) also modulated the effect of aridity and plant-plant interactions on species abundances. The importance of facilitation to drive species abundances decreased with aridity, as species preferred arid conditions and did not need neighbours to thrive. Instead, competition showed stronger relationships with species abundances under high levels of aridity. As composition became dominated by aridity specialists, the importance of aridity in shaping dryland plant communities did not increase further from moderate to high aridity levels.
4. *Synthesis*: Our results showed that: i) the degree of community specialization to aridity mediates the relative importance of plant-plant interactions in determining species abundances and ii) facilitation and competition were more strongly related to species abundance in communities dominated by generalists and specialists, respectively. We observed a shift from facilitation to competition as drivers of species abundances as aridity increases in global drylands. Our findings also pave the way to develop more robust predictions about the consequences of ongoing climate change on the assemblage of plant communities in drylands, the largest terrestrial biome.

KEY WORDS:

plant community diversity and structure, community assembly drivers, facilitation, specialisation, niches, competition, drylands

INTRODUCTION

A major challenge in ecology is to accurately predict community composition to better understand how climate change will impact ecosystem structure and functioning (Chapin III *et al.* 2000). Central to this challenge is to evaluate the interplay between macro- (climate, dispersion) and micro- (biotic interactions) scale determinants of species relative abundance (Lawton 1999; Soberón 2007; Mayfield & Levine 2010; Shipley 2015). Previous studies on this topic have mostly focused on plant species richness, and this has undoubtedly contributed to our understanding on how plant communities are responding to ongoing climate change (Cavieres *et al.* 2006; Valiente-Banuet & Verdú 2007; Wright *et al.* 2017). However, measuring species richness alone may not suffice as an indicator of changes in diversity (Lyashevska & Farnsworth 2012; Dornelas *et al.* 2014). Within communities, shifts in composition may have effects on ecosystem functioning that are equal to, or stronger than, the effects of shifts in species richness (e.g., Shi *et al.* 2016; Hillebrand *et al.* 2017; Spaak *et al.* 2017). Thus, assessing drivers that alter species relative abundances is of paramount importance to understanding how these compositional changes will affect communities and ecosystem functioning in response to ongoing climate change.

Combining approaches that focus on contrasting spatial scales can help in assessing the interplay between these macro- and micro-scale determinants of community structure (Fig. 1). Based on environmental suitability, which is typically evaluated at large spatial scales, species distribution models (SDMs hereafter) can help to identify the upper limit of species abundance within a community (VanDerWal *et al.* 2009; Butterfield & Munson 2016). Along with their ability to describe the environmental suitability, SDMs allow us to assess the species ability (strategy) to cope with the local environmental conditions, an important parameter to predict the outcomes of biotic interactions (Liancourt, Callaway & Michalet 2005; Gross *et al.* 2010). Spatial co-occurrence patterns, in turn, are typically applied at local scales, and can inform us about the frequency and strength of micro-scale determinants of species abundance (notably plant-plant interactions, e.g., Cavieres *et al.* 2006). However, they provide limited information about the role of abiotic factors to determine species abundance. Due to their complementary properties, the combination of SDMs and local co-occurrence patterns is being increasingly used to assess the relative importance of these biotic interactions in species distribution models (e.g. by including co-occurrence matrices on SDMs; Boulangeat *et al.* 2012; Wisz *et al.* 2013; Godsoe *et al.* 2017), or to infer the relative importance of habitat sharing on co-occurrence patterns (Steinbauer *et al.* 2016). Combining these approaches can help in understanding the interplay between climatic factors, plant-plant interactions and species-specific responses as drivers of local species abundance. However, such combination of methods has not yet been used to evaluate how the relative importance of the different drivers of species´ abundances changes along large environmental gradients.

Drylands (i.e., areas in which the ratio between precipitation and evapotranspiration is lower than 0.65, Middleton & Thomas 1992) are particularly well-suited to investigate the relative importance of multiple determinants of the local abundance of plant species. Aridity and plant-plant interactions (competition and facilitation) interact to shape the composition and diversity of dryland plant communities in complex ways (Tielbörger & Kadmon 2000; Tirado & Pugnaire 2003; Soliveres & Maestre 2014). Indeed, previous studies have focused on how plant-plant interactions and abiotic factors will interact to affect plant species abundance and diversity in the future (e.g., Michalet *et al.* 2006; Holmgren & Scheffer 2010; Soliveres & Maestre 2014; Butterfield & Munson 2016). Some of these studies suggest that positive interactions between species (facilitation) may become more frequent with increasing aridity, buffering the negative impact of climate change on plant diversity (Callaway 2007). Others, in turn, predict a collapse of facilitative interactions in the most extreme environments, which would multiply the adverse effect of extreme climates on plant diversity (Michalet *et al.* 2006; Holmgren & Scheffer 2010). Both competition and facilitation could also remain strong across environmental gradients, with the identity of the resources plants compete for shifting from above- to below-ground (Tilman 1982).

Furthermore, compositional changes are the norm across environmental gradients, and these could modulate how the environment and plant-plant interactions shape plant communities. For example, it has often been questioned whether the changes in the sign and frequency of plant-plant interactions across environmental gradients are driven by the environment itself, or by the changes in species composition along the studied gradients (e.g., Hacker & Gaines 1997; Gross *et al.* 2010; Soliveres & Maestre 2014; Liancourt *et al.* 2017; Qi *et al.* 2018). Additionally, compositional shifts towards communities dominated by species specialized to thrive under arid conditions could make plant communities less sensitive to further increases in aridity (Ulrich *et al.* 2014). Species exhibiting preference for arid conditions may be more competitive under aridity ranges in which they are better suited (Goldberg & Novoplansky 1997), and less dependent from facilitative interactions (Gross *et al.* 2010). However, the role of aridity preferences as modulators of the drivers of community assembly across environmental gradients has not yet been investigated at a global scale.

We gathered data from 157 drylands worldwide, and combined SDMs with local co-occurrence approaches to investigate the interplay of aridity, plant-plant interactions (inferred using co-occurrence patterns) and the degree of preference of species to local aridity conditions (assessed with aridity niches extracted with SDMs) as drivers of species relative abundance within dryland plant communities. We hypothesized that i) aridity and plant-plant interactions will interact to drive species relative abundance, an interaction that will be influenced by the match between the aridity preference of species and local aridity of the sites in which they are living; ii) species composition becomes more specialised to aridity as aridity increases; and iii) in communities dominated by species specialised to high aridity conditions, facilitation is less important than competition as a determinant of species abundance.

MATERIAL AND METHODS

Study sites and field sampling

The 157 drylands studied are a subset of the 236 sites surveyed by Ochoa-Hueso *et al.* (2018), and were located in 19 countries from six continents (Fig. S1). They widely differ in their environmental conditions, with annual mean temperature, rainfall and elevation ranging from -1.8 to 27.8 ºC, from 67 to 1219 mm, and from 69 to 4668 m a.s.l., respectively. Our database includes grasslands, shrublands and savannahs, with species richness ranging from 2 to 52 perennial species, and total plant cover ranging from 2 to 82 %.

All the sites were surveyed between 2006 and 2013 according to a standardized sampling protocol (see Maestre *et al.* 2012 for details). In each of these sites a 30 m x 30 m plot was established and within each plot we established four parallel 30 m long transects at 8 m intervals. We established 20 quadrats (1.5 x 1.5m) along each transect (80 per site) and visually estimated in each quadrat the cover of each perennial plant species, which we used as a surrogate of species abundance. A total of 898 species were identified to the species level. We calculated the aridity level of each site as 1 − aridity index (AI), where AI is the precipitation/potential evapotranspiration ratio. We obtained the Aridity index from the Global Potential Evapotranspiration database (Zomer *et al.* 2008), which is based on interpolations provided by WorldClim (Hijmans *et al.* 2005).

Evaluating aridity and plant-plant interactions as drivers of species abundances

We developed a four-step approach (steps i to iv) to evaluate how macro- and micro-scale factors determine species relative abundances in the plant communities studied. First, we extracted a function that related the suitability of each species to aridity (aridity niche hereafter) using SDMs. This provides us the hypothetical local relative abundance of species expected when considering only macro-scale factors (i.e., the match between aridity preferences of the species and local aridity conditions). Secondly, we evaluated the effects of both macro- and micro-scale (plant-plant interactions, as extracted from co-occurrence analyses) determinants of the relative abundance of species within each community and tracked changes in their relative importance along an aridity gradient. Thirdly, we estimated the main features of species niche (niche optimum, niche breadth and niche skewness), calculated a community-weighted mean of such features, and evaluated their variation along aridity gradients to identify changes in common strategies of species specialisation to aridity. Finally, we evaluated changes in the importance of macro/micro scale determinants of species relative abundance (step ii) along a gradient of community specialisation to aridity (obtained from step iii).

We obtained global presence/absence data for each species, necessary to perform step i, from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). We used species cover measured in the field as our estimate of the local abundance of each species (necessary to perform steps ii, iii and iv), and the 80 quadrats per site to calculate co-occurrence metrics (step ii). Each step is described in detail below.

Step i - Assessing aridity niches using species distribution models

SDMs are nonlinear statistical models relating abiotic variables (predictors) with species occurrences (response variable) at regional or global scales. We used a gradient analysis using GBIF-obtained species occurrences as response variable and aridity as the sole abiotic factor. This constitutes the simplest version of SDMs from which we attempt to calculate an estimate of expected abundance according to the response of each species to aridity (Austin, Nicholls & Margules 1990). Aridity is a good proxy for water availability, which is the most influential abiotic factor for plant survival in drylands (Whitford 2002), and is a key determinant of both species interactions and community composition in these environments (Callaway 2007; Ulrich *et al.* 2014). Additionally, aridity combines into a single measure temperature and precipitation, both important factors affecting community assembly as shown in other studies using SDMs in drylands (Butterfield 2015; Butterfield & Munson 2016). Nevertheless, our results remained very similar when using aridity niches after considering additional environmental variables related to rainfall seasonality, soil attributes and low temperatures (Appendix S2).

We performed gradient analyses using General Additive Models (GAM, reviewed in Austin 2007) as described in full in Appendix S1. Based on these niches, we then estimated the "aridity-driven abundance" (AAb), i.e., the expected local relative abundance of each species, based solely on the aridity level of each site and the other species able to colonize it (see Fig. 1.a), as:

$$AAb_i = \frac{SP_i}{\sum_{j=1}^{nsp} SP_j} \qquad \textbf{equation 1}$$

where nsp is the number of species in the community. SP is species performance (a surrogate of each species´ preference for the local aridity), interpolated from its aridity niche. To ensure the comparability of SP data, we standardized niches to their maximum (thus it ranged between 0 and 1 for each species). This methodology assumes that for a particular environmental condition, a species will share the available space with its neighbours by occurring proportionally to its aridity preferences (as measured with the aridity niches). We assumed that relative abundances in the community emerge from sampling the species pool according to the local aridity level. Therefore, the relative abundance, driven by macro-scale factors, is the density expectation of sampling all species present in the community, each with a probability that depends on its SP.

Since SDMs are calculated at large spatial scales, we expect them to mostly reflect the effects of abiotic conditions on the abundance of each species (Pearson & Dawson 2003). However, SDMs can be partially influenced by biotic interactions (Wisz *et al.* 2013) and this limitation should be considered when interpreting our results (see *Study limitations* in the Discussion).

Step ii – Developing a statistical model to predict species relative abundance

-Plant-Plant interactions: Expected abundance using co-occurrence matrices

For each site, we obtained an estimate of the expected relative abundance of each species according only to plant-plant interactions (measured as spatial co-occurrences). To do so, we used aggregation/segregation as proxies of facilitation/competition, respectively (Tirado & Pugnaire 2003; Cavieres et al. 2006; Valiente-Banuet & Verdú 2008). Co-occurrence measures have been successfully linked to plant-plant interactions as estimated from manipulative studies (Tirado & Pugnaire 2003), and is the only method available when experimental manipulations are logistically challenging due to the large number of sites and/or species (Cavieres *et al.* 2006; Valiente-Banuet & Verdú 2008). However, spatial co-occurrences can also be driven by other factors such as habitat sharing or seed capture (Morales-Castilla *et al.* 2015; Delalandre & Montesinos-Navarro 2018), which could overestimate facilitation in our study.

As a metric of spatial aggregation/segregation, we obtained a normalized score of co-occurrence using PAIRS (Ulrich 2008). PAIRS randomizes the matrices of species occurrences within the quadrats of each site and detects deviations from random spatial association patterns in all species pairs while controlling for the existence of false positives due to multiple testing. We used the abundance of each species in each of the 80 quadrats per site surveyed, and the abundance-weighted swap method, to perform these randomizations. This method assumes sampling quadrats with equal probabilities of being colonized and keeps species richness and local abundances constant to account for overall differences in habitat suitability. We obtained co-occurrence in both observed vs. randomized communities for each species pair, in each community, as:

$$Co-occurrence_{ij} = (n_i - N_{ij})(n_j - N_{ij}) \qquad \textbf{equation 2}$$

where n is the number of occurrences of target species (n_i) and each of its neighbours (n_j), and N is the number of co-occurrences of both species together. We used the standardized effect sizes obtained from comparing co-occurrences of the null model with those observed in the field as a metric of the strength of the interaction between target species and their neighbours. Standardized effect sizes are comparable between different pairs, but do not take into account how frequent the interaction is within the community. To correct for this, we estimated the relative abundance of species *i* expected due to competition (i.e., negative co-occurrence, equation 3) and facilitation (i.e., positive co-occurrence, equation 4) with other species (j, not including i) as:

$$Cab_i = \sum_{j=1}^{nsp} |\beta_{j\to i}| * p_j \quad iff\ \beta_{j\to i} < 0 \qquad \textbf{equation 3}$$

$$Fab_i = \sum_{j=1}^{nsp} \beta_{j\to i} * p_j \quad iff\ \beta_{j\to i} > 0 \qquad \textbf{equation 4}$$

Where, Cab and Fab represent the competition and facilitation-driven abundances, respectively, for each species in the community; β represents the standardized effect sizes obtained measuring the competitive (if negative) and facilitative (if positive) effect over species *i* of other species in the community (*j*), and p_j represents the relative abundance of species *j* in the surveyed community. By doing this we obtained a metric of the effect of plant-plant interactions on the abundance of the target species for a specific community. This metric is considering both the strength of the interaction with each neighbour (standardized effect sizes) and the frequency of such interactions within the community (relative abundance of the neighbours).

-Fitting the statistical model

We used linear mixed models to analyse the relative abundances of each species as a function of: i) aridity-driven abundance (AAb), ii) cumulative effects of both competition-driven (CAb) and facilitation-driven (FAb) abundances, and iii) the height of the target species (equation 5, Fig. 1.c). Plant height was only introduced to control for potential confounding effects between cover (used to estimate relative abundance in the field) and the size of the species being sampled (taller species are more likely to score higher cover values regardless of their abundance, Falster *et al.* 2011). Plant height was obtained from available databases, published literature and local floras (see Appendix A from Soliveres *et al.* 2014 for a full reference list). To account for species-specific differences within a community and for species similarities among communities we included "species identity" as a random factor in the model. In addition to aridity and plant-plant interactions, we also considered average phylogenetic distance between each target species and its neighbours, and rarity (obtained from the number of GBIF occurrences), as known drivers of plant-plant interactions (e.g., Valiente-Banuet & Verdú 2008; Soliveres *et al.* 2015). However, since these additional predictors did not change the main results presented here (Appendix S3) we focus on the simplest models to test our hypotheses more clearly.

Species' preference for the local environment may influence the importance of facilitation and competition (Choler, Michalet & Callaway 2001; Gross *et al.* 2010; Soliveres *et al.* 2014; Liancourt *et al.* 2017). Therefore, we established an interaction between aridity- (AAb, derived from the niches and summarizing each species´ preference for the local aridity), competition- and facilitation-driven abundances. Interactions between aridity-driven abundance and competition/facilitation will be positive if the effect of plant-plant interactions on species abundance is higher for species showing high preference for local aridity conditions (high AAb) than for species not showing that preference for local aridity conditions (low AAb). It must be noted that the effects of competition are negative, therefore positive contributions from the interaction term decrease the significance of the effect of competition on the relative abundance of species adapted to local aridity conditions. Thus, our final model was:

$$AbRel_i = AAb_i + FAb_i + CAb_i + AAb_i * FAb_i + AAb_i * CAb_i + size_i + (1|sp_i)$$

equation 5

Where *AAb*, *FAb* and *CAb* represent aridity, facilitation and competition-driven abundances, respectively. Size is the height of species *i*. We obtained the standardized effect sizes of all variables on relative abundance. We assume that the effect size of how suitable the local aridity is for a given species (AAb) and plant-plant interactions on relative abundance represent the relative importance of aridity filters and plant-plant interactions, respectively, as drivers of species relative abundance.

We performed this statistical model using all the species of all our sites to assess the relative overall contribution of each determinant of species relative abundance in all the drylands studied.

-Evaluating changes in the relative importance of macro/micro scale determinants of species relative abundance along aridity gradients.

We first ordered all the sites surveyed according to aridity. Then, we took the 45 sites with the lowest values of aridity (as this number of sites allowed sufficient statistical power for our model), and performed the mixed model described in equation 5 (see Fig. 1d). We then bootstrapped the standardized slopes of each predictor to obtain their confidence intervals, which were matched to the average value of aridity across the 45 sites. Next, we removed the community with the lowest value of aridity from the 45 selected sites, and added the community scoring the next higher value to repeat the same calculations. We repeated this loop as many times as sites remained (112). The coefficients of the standardized predictors included in the linear mixed models provide a comparable measure of the importance of plant-plant interactions and the position of each species regarding its aridity niche. We used the 95 % confidence interval to assess changes in the importance of macro/micro scale determinants of species relative abundance across the aridity gradient.

Step iii – Identifying dominant plant strategies based on niche features

Aridity niches hold information about the adaptive strategy of species by describing the following features: i) niche optimum, the aridity level at which a species performs optimally (i.e. SP = 1); ii) niche breath, the aridity range that a given species occupies; and iii) degree of specialization to aridity conditions, as measured by the skewness of aridity niches (see examples in Fig. S2). As this information is available for each species, each niche feature can be considered to be an attribute of the species and related to its overall response to aridity. These attributes can be used to scale the response of species to aridity at the community level, i.e., to track how species composition changes across the global aridity gradient that we studied (see a similar approach in Butterfield & Munson, 2016).

We first calculated the community weighted mean niche optimum (CW-niche optimum) as a measure of the average aridity preference of the species forming each community. CW-niche optimum was obtained as the sum of the niche optimum of species weighted by their observed relative abundance (adapted from Lavorel & Garnier 2002), and was used to evaluate how well the optimum level of aridity of the species forming each community matched the aridity observed in the sites. Differences between CW-niche optimum

and observed aridity may affect the importance of aridity-driven abundance as a community assembly driver, as it indicates extra stress for the species forming the community. We used this analysis to understand variations in the importance of aridity-driven abundance (see step ii) across aridity gradients.

Secondly, we calculated the community weighted mean of niche breath (CW-Niche breadth) and shape (CW-Niche skewness) to assess the degree of specialisation to aridity of a given plant community. A small CW-Niche breath identifies communities that are specialised to a particular range of aridity conditions, whereas the shape informs us about the preference of such community for more or less arid environments. Hence, communities dominated by species that are specialised to aridity will be identified by a lower CW-Niche breath and a negative CW-Niche skewness (i.e., right-skewed, indicating a preference for high aridity levels). We observed a strong correlation between niche breadth and skewness ($r > 0.60$). Communities dominated by species with a narrow niche breath also tend to be dominated by species with a negative skewness (Fig. 2). Therefore, we only used CW-Niche skewness as a measure of the community specialisation towards arid environments (community specialisation hereafter).

Step iv –Exploring changes in the relative importance of macro/micro-scale determinants of species relative abundance across a gradient of community specialisation

We used the same approach already described in the last section of step ii ("track micro/macro scale determinants of species relative abundance along aridity gradients"), but using this time CW-Niche skewness obtained in step iii instead of aridity.

In the case of community specialisation, we did not use the interaction terms described in equation 5. We did so because CW-Niche skewness partly summarizes the influence of species aridity preferences on the importance of plant-plant interactions and, therefore, the information extracted from interaction terms is redundant with that extracted from the gradient.

Further statistical details

To maintain information representative of the community level in the analyses described in steps ii, iii and iv above, we used all sites for which we gathered enough information (e.g., discarding species with less than 20 occurrences in GBIF [see Appendix S1], or those for which we could not retrieve height values) for the species that summed up at least 60 % of the total perennial vegetation. A total of 157 out of the original 236 communities remained for further analyses, leaving a total of 1631 study cases (405 different species in 157 communities with some species repeated throughout communities). The species from these communities represented on average 91.6 ± 10.3 % (mean ± SD) of the total cover of perennial plants in the surveyed sites.

Mixed models in steps ii and iv were performed using the "lme4" R package (Bates *et al.* 2015) in R (R Development Core Team 2008). We log-transformed all variables but aggregation and segregation (which were double square root-transformed), and scaled the values after transformation to: i) fulfill the assumptions of the analyses and ii) obtain standardized coefficients. We extracted the marginal (variance explained by fixed factors) and conditional (variance explained by fixed + random factors) R^2 values (Nakagawa & Schielzeth 2013) using the "piecewiseSEM" R package (Lefcheck 2016).

For the analyses described in steps ii and iv above, we used Generalized Additive Models (Wood 2006) to depict smoothed trends in the effects of the different drivers of species abundances across gradients of aridity and community specialisation. These models are used to investigate the nonlinear relationships and work well when a large number of replicates is considered (Wood 2006). Data and code used to perform all the analyses are available in figshare (Berdugo *et al.* 2018).

RESULTS

Changes in the relative importance of aridity and plant-plant interactions as drivers of species relative abundance

The strongest predictors of species relative abundance in our models were facilitation (measured as positive co-occurrences) and aridity-driven abundance, which exhibited similar effect sizes (Fig. 3). Competition (negative co-occurrences) and the interactions between aridity-driven abundance and plant co-occurrences showed negative effects in the overall model. The negative effects of interaction terms suggest that species well suited to local aridity in drylands usually experience less facilitative and more competitive effects.

The importance of aridity-driven abundance as an assembly driver increased up to aridity levels ~ 0.75 (i.e., the limit between arid and semiarid climates), and stabilized beyond that value (Fig. 4a). The effect of facilitation declined linearly, while that of competition increased (i.e., became more negative), with aridity. However, the effect of competition was only significant under very high aridity levels (0.75-0.80) and only at some levels of the moving window. The interaction term between aridity-driven abundance and competition shifted throughout the aridity gradient from negative (at wetter sites) to positive (at dryer sites). These results indicate that, in the less arid sites of our gradient, competition was less important for species showing high preference for local aridity than for those less suited to local aridity. Conversely, at high aridity levels, the effects of competition were stronger for species showing high preference to local aridity than for those that were far from their aridity optimum. The interaction term between responses to aridity and facilitation turned negative with increasing aridity, although it was statistically significant only at some points of the gradient (Fig. 4b). This result suggests that, under high aridity conditions, facilitation tends to be a more important driver of species abundances for those species not suited to the local (high arid) conditions. These results remained qualitatively consistent when using niches obtained by controlling other abiotic variables to calculate AAb, when using other statistical tools to extract niches such as MAXENT (Appendix S2), or when adding other variables related

with community assembly into the model (e.g., average phylogenetic distance and rarity, see Appendix S3).

Common strategies on species adaptive response along aridity gradients

The relationship between the CWM of aridity optima and observed aridity was close to the 1:1 line (slope = 0.8 ± 0.19), but deviated from this line at intermediate aridity levels (about 0.6-0.8; Fig. 2a). The decrease in both CW-Niche breadth and CW-Niche skewness (i.e. the occurrence of right-skewed niches) within this aridity range suggested that species forming the community became more specialised to arid conditions (Fig. 2b and 2c). All these trends were not confounded by the uneven distribution of the number of communities across the aridity gradient studied (Fig. S3).

As communities became dominated by aridity-specialist species, the effect of facilitation on species´ relative abundance declined, while that of competition and aridity-driven abundance increased (Fig. 5). The decline in the importance of facilitation was abrupt and became not significant around values of skewness = 0, thus representing symmetrical niches.

DISCUSSION

We investigated shifts in the relative importance of macro- (aridity niches) and micro- (plant-plant interactions) scale determinants of species relative abundance along a global aridity gradient, accounting for the aridity preferences of the species forming each community. We found that facilitation (estimated from positive spatial co-occurrences) and aridity (estimated from the realized niches of aridity) were stronger predictors than competition (measured as negative spatial co-occurrences) in explaining local species abundances. However, the shift from communities with species exhibiting a wide range of aridity preferences towards communities dominated by specialist species with increasing aridity substantially reduced the importance of facilitation and reduce further the effect of increasing aridity in determining the relative abundance of species within communities. Our study provides fundamental information on the drivers of dryland species abundances, and, may help to forecast future community composition in response to climate change in these areas.

Facilitation as a driver of species relative abundance in drylands

Facilitation and aridity were the two main drivers of dryland species abundances. The importance of facilitation peaked at moderate aridity conditions (1-AI < 0.7) and for generalist communities (Fig. 5). Our results reinforce the view that facilitation not only promotes the abundance of rare species, but also of dominant ones (Gross *et al.* 2010; Le Bagousse-Pinguet *et al.* 2014). We speculate with the possibility that facilitation was especially high under moderate aridity conditions because of the evolutionary history of these sites. Previous studies have reported that species from the tertiary period benefit from facilitation by species that originated later in the quaternary (when conditions became harsher, Valiente-Banuet *et al.*

2006). Therefore, in places with intermediate aridity, where we would find mixes of species from both evolutionary lineages, is where facilitation is expected to contribute most to species abundance due to facilitation of mal-adapted species from the tertiary. On the other hand, large ranges of some dryland species (i.e.; appearing as generalists) might result from the effect of facilitation, which can expand species niches (Bruno, Stachowicz & Bertness 2003; Wisz *et al.* 2013; Stewart *et al.* 2015; Tikhonov *et al.* 2017). Following this rationale, this is probably the reason why we could not see interactions between facilitation and aridity-driven abundance (which would indicate that facilitation especially benefit species not suited to local aridity conditions) until aridity exceeds 0.6. Our results, therefore, suggest that niches of species living under intermediate aridity conditions might have been expanded by facilitation.

Changes in the importance of macro/micro-scale determinants of species relative abundance across aridity and specialisation gradients

Our results, support the occurrence of a tight coupling between the degree of community specialisation and the outcomes of plant-plant interactions within plant communities, at a spatial scale never tested before. Our SDMs indicated that species niches became narrower and more skewed towards dry conditions at aridity levels > 0.7 (Fig. 2). This suggests that communities are dominated by highly specialized species under the most arid conditions, likely as an adaptive response of the species to increasing environmental harshness (Noy-Meir 1973; Devictor *et al.* 2010). In a recent study, Butterfield & Munson (2016) found that temperature niches are usually symmetrical around the optimum value and that they were more important than precipitation niches as a driver of community assemblage. We focus here on aridity, which is a composite of both precipitation and temperature. Therefore, we would expect the degree of community specialisation to be a function of how species dominating the community respond to the interaction between temperature and precipitation, rather than to their response to either factor separately (Butterfield & Munson 2016). An alternative explanation to our contrasting results is that our study covers a larger range of climatic conditions and specialisation levels than that of Butterfield & Munson (2016), which would explain why our niches were less symmetrical and the effect of precipitation was stronger than previously observed.

The importance of including the degree of specialisation of the species pool to accurately forecast compositional shifts with climate change has been highlighted before (Bush *et al.* 2016). Our study builds on these findings to show the response of dryland plant communities to further aridification. Following the increase in specialisation, we found a unimodal trend on the importance of aridity-driven abundance in the most arid drylands (Fig. 4a for aridity > 0.75, Fig. 5). These results suggest that communities that are already experiencing high levels of aridity should not be expected to drastically shift their composition with further aridification (but see Butterfield 2015). This is consistent with the low levels of species turnover found in our most arid communities (Ulrich *et al.* 2014), suggesting that fewer changes in community composition occur at the highest levels of aridity in our database. Interestingly, resilience of both productivity and stability in drylands has been strongly linked to plant compositional changes (e.g., Gherardi & Sala 2015; Shi *et al.* 2016), which suggests

that the compositional "stand-by" we observed at high aridity levels could potentially have negative effects on other properties of dryland ecosystems.

Compositional shifts towards communities dominated by aridity-specialists affected the relative importance of plant-plant interactions at the community level (Fig. 5, Fig. S4). Indeed, we found a strong decrease in the importance of facilitation as a driver of plant species abundance from aridity levels of 0.75-0.80 onwards, supporting previous studies that focused on pairwise interactions (e.g., Cavieres *et al.* 2006). These results are likely caused by a higher specialisation of the species pool under high aridity conditions, with species well adapted to their local conditions less likely to benefit from the presence of neighbours (Michalet *et al.* 2014; Liancourt *et al.* 2017). The relative abundance of species living in communities dominated by specialist species is less dependent on facilitation and more on competition, as suggested by experimental (e.g., Liancourt *et al.* 2005; Gross *et al.* 2010) and theoretical (Michalet *et al.* 2014) studies. As specialists became dominant in high aridity sites (Fig. 2b and c), the effect of facilitation declined, and that of competition increased, along the aridity gradient evaluated (Fig. 4a). Note that under high aridity conditions, facilitation was still more important for species not showing high preference to local aridity conditions than for those more suited to them (Fig. 4b). Overall, our results support the notion that facilitation is less important for species adapted to local conditions, and that plant-plant interactions depend more on the species-specific aridity preferences than on the overall environmental harshness (Soliveres & Maestre 2014; Liancourt *et al.* 2017).

Our analyses identified a shift in the relative importance of facilitation and competition at aridity levels of ~0.75-0.80. Studies that have focused on the relationship between facilitation and species richness have not found a collapse in facilitation along similar aridity gradients to those studied here (Soliveres & Maestre 2014). This suggests that the impact of plant-plant interactions may differ depending on whether we focus on contrasted facets of the community (i.e. species richness *vs.* changes in relative abundances). In addition, our results help to explain why the spatial patterns of dryland vegetation decouple from facilitation under aridity levels ≥ 0.8 (Berdugo *et al.* 2017). Under these conditions, facilitation is no longer an important driver of species abundance, which is likely related to the size of plant patches in drylands (Xu *et al.* 2015; Berdugo *et al.* 2017). Previous studies have failed to link facilitation with ecosystem functioning (Maestre *et al.* 2010), probably due to the focus on the relationship between facilitation and species richness as the sole mechanism linking these ecosystem properties (but see Mitchell, Cahill & Hik 2009). Facilitation is known to affect spatial patterns, which are fundamental drivers of ecosystem functioning in drylands (Maestre *et al.* 2016; Berdugo *et al.* 2017). Thus, we speculate that focusing on the links between facilitation and species abundance, and therefore on spatial patterns, could provide the long hypothesized but largely untested link between facilitation and ecosystem functioning. In this regard, our study also highlights that abiotic factors may limit strongly the identity of species living in extremely arid conditions, which role on conditioning low functionality levels is worth further exploration.

Study limitations

Inferring processes from any observational study is challenging. First, we assumed that SDMs reflect the effect of abiotic conditions on the abundance of each species (Pearson & Dawson 2003). Our data supported this assumption, as the fit between species´ optima to aridity (as obtained with the community-weighted mean optimum) fitted well with the local aridity conditions in each community (Fig. 2a). However, SDMs can be partially influenced by biotic interactions (Wisz *et al.* 2013) and, although we controlled for this influence of biotic interactions by including surrogates of plant-plant interactions in our analyses, this limitation should be considered. Second, we derived our measures of facilitation and competition from spatial co-occurrence metrics. Co-occurrences are related to plant-plant interactions as estimated from manipulative studies (Tirado & Pugnaire 2003), but could also be driven by other factors such as habitat sharing or seed capture (Morales-Castilla *et al.* 2015; Steinbauer *et al.* 2016). Moreover, and contrary to most assumptions, strong competition could also cause aggregated patterns if the species involved are competing for a shared resource (e.g., water) in a particular microsite where species are more strongly limited by different resources (e.g., niche differences caused by soil nutrients, see also Sears & Chesson 2007; Adler, Ellner & Levine 2010; Godoy, Kraft & Levine 2014). In this regard, the patterns found in our study suggest that niche differences in the high aridity sites might have forced niche species to have fewer degrees of freedom (i.e., they need to compete mostly for water, thus resulting in fewer axes of variation in the niches that would allow stabilizing niche differences). Therefore, we hypothesize that stabilizing competition is also expected to be less frequent with increasing aridity (i.e., would follow the same trend as facilitation in our study).

Finally, aridity and plant-plant interactions explained little variation in species abundance in our overall model (marginal $R^2 = 0.15$). This is not unexpected in such large-scale studies or where diverse habitat-types and biogeographical regions are included, and suggests that other factors not controlled in this study (e.g., dispersal mode or functional traits, indirectly accounted for by the "species" random factor) may drive important changes in the abundance of dryland plants. The interplay between these assemblage factors and the abiotic/biotic assemblage drivers included here should be considered in future studies aiming to accurately determine species relative abundances.

CONCLUDING REMARKS

Our results emphasizes species adaptation to aridity as a modulator of the role of environmental filters and plant-plant interactions as drivers of community assembly. They suggest that the composition of arid plant communities may be highly resilient to further increases in aridity, and that facilitation (inferred from spatial aggregation) was more important for species whose aridity preferences do not match local conditions than for those species well suited to local aridity in drylands. We found shifts from facilitation- to competition-driven communities at aridity levels around 0.7, with potentially important cascading effects on ecosystem functioning that deserve further attention. Our findings can be used to refine forecasts of plant community composition under climate change in drylands, the largest biome on Earth.

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AUTHOR'S CONTRIBUTION

F.T.M. designed the sampling design and coordinated field data acquisition. M.B. and S.S. designed the study. Data analyses were done by M.B, assisted by S.S. The paper was written by M.B., and all authors substantially contributed to the subsequent drafts.

DATA ACCESSIBILITY

Dataset used in this study and R codes used to perform analyses are available through figshare (Berdugo *et al.* 2018).

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FIGURE LEGENDS

Figure 1. Summary of the methodological approach used. We first obtained, for each species, the aridity-driven abundance using species distribution modelling with aridity as predictor (A) and plant-plant interactions (using spatial co-occurrences measured in the field as a proxy, B). We then modelled the relative abundance of species (response variable) using aridity-driven abundance and plant-plant interactions, additionally controlling for species size (C). The effect of each of these predictors on species abundance describes the importance of each assembly driver evaluated (aridity, facilitation and competition) for community assembly. Finally, we used a moving window approach to explore how the importance these assembly drivers changes along aridity and community specialisation gradients (D). SP: Species Performance, STD: Standardized coefficients. * Height was included only to control for sampling effects (see Methods).

Figure 2. Relationships between aridity and the community weighted mean (CWM) of the niche optimum (a), breadth (b) and skewness (c) obtained from species distributions models. The blue line and shaded area are the gam-smoothed trends (non-parametric regressions) observed ± 95 % confidence interval, respectively. The black line in a) represents the 1:1 line; and the CWN (Niche Skewness) = 0 in c) indicates the point at which skewness changes direction.

Figure 3. Standardized effect sizes of different drivers of species relative abundance obtained from the linear mixed model applied to all dryland communities. Median, 50 and 75 quantiles are represented in a box plot for each effect. Marginal (variance explained by fixed factors) and conditional (variance explained by fixed + random factors) R^2 values are shown.

Figure 4. Standardized effect sizes of facilitation, competition and aridity-driven abundance (a) and the interactions between aridity-driven abundance and competition and facilitation (b) as drivers of species relative abundance along an aridity gradient. This analysis is performed by fitting a linear mixed models throughout a moving window in a subset of the sites surveyed following our aridity gradient. Bootstrapped coefficients of this regression with their 95% confidence intervals are shown for each step of the moving window. Lines represent the gam-smoothed trends of variation of the effect sizes.

Figure 5. Standardized effect sizes of facilitation, competition and aridity along a gradient of community specialisation (measured as community weighted [CW] niche skewness). This analysis is performed by fitting a linear mixed model throughout a moving window in a subset of the sites surveyed following a gradient of community specialisation. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines represent the gam-smoothed trends of variation of the effect sizes.